

# Male burying beetles extend, not reduce, parental care duration when reproductive competition is high

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## Abstract

Male parents spend less time caring than females in many species with biparental care. The traditional explanation for this pattern is that males have lower confidence of parentage, so they desert earlier in favour of pursuing other mating opportunities. However, one recent alternative hypothesis is that prolonged male parental care might also evolve if staying to care actively improves paternity. If this is the case, an increase in reproductive competition should be associated with increased paternal care. To test this prediction, we manipulated the level of reproductive competition experienced by burying beetles, *Nicrophorus vespilloides* (Herbst, 1783). We found that caregiving males stayed for longer and mated more frequently with their partner when reproductive competition was greater. Reproductive productivity did not increase when males extended care. Our findings provide support for the increased paternity hypothesis. Extended duration of parental care may be a male tactic both protecting investment (in the current brood) and maximizing paternity (in subsequent brood(s) via female stored sperm) even if this fails to maximize current reproductive productivity and creates conflict of interest with their mate via costs associated with increased mating frequency.

## Introduction

In most species with biparental care, females spend more time caring than males (Kokko & Jennions, 2012). The reason why male parents desert before females and why they vary in the length of time they stay with their caring partner is often unclear (Kokko & Jennions, 2012). Regardless of intersexual differences in prenatal reproductive costs (such as egg vs. sperm production), offspring fitness benefits associated with increased post-natal parental effort should be shared by both parents, all else being equal. Conflict of interests between parents occur because parental care is costly: it takes time that could be used in trying to find more mating opportunities, and energy invested in current offspring may trade off with future reproductive productivity (Clutton-Brock & Vincent, 1991; Royle *et al.*,

2012). As a result of these costs, each individual parent stands to gain in the future if they can minimize their own current effort at the expense of their partner (Trivers, 1972; Parker *et al.*, 2002; Royle *et al.*, 2002; Harrison *et al.*, 2009).

This paradigm has been used to explain variation in the level of male care: maternity is typically more assured than paternity in species with biparental care (Alonzo & Klug, 2012). Consequently, selection is expected to disfavour males that care for offspring unrelated to themselves (Whittingham *et al.*, 1992; Houston, 1995; Kokko & Jennions, 2008; Alonzo & Klug, 2012) and/or favour paternity protection behaviours such as mate guarding or high mating frequency that counter the threat from sperm competition (Birkhead, 1979, 1982). A general, positive relationship between paternity assurance and paternal effort has been found across species (Griffin *et al.*, 2013), and within species, cues indicating declining paternity assurance may select for facultative adjustment in paternal care (Sheldon, 2002; Kokko & Jennions, 2008). Empirical evidence exists that shows males

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decreasing parental effort when they obtain fewer matings (e.g. Burke *et al.*, 1989; Hartley *et al.*, 1995) or when risks of cuckoldry increase (e.g. Hunt & Simmons, 2002; Benowitz *et al.*, 2013), but overall support for the relationship between paternity assurance and paternal effort is mixed (Alonzo, 2010).

An underlying assumption is that male care is driven by improved parental productivity and/or indirect benefits through increased fitness of offspring, but an alternative hypothesis is that males stay if this increases the proportion of their paternity in current and/or future broods, rather than providing care *per se* (Kvarnemo, 2006; Kahn *et al.*, 2013). This 'increased paternity' hypothesis casts male parental care in a different light: male care need not be beneficial to offspring, and it may create additional conflict of interests between mates. Under this scenario, male care in the current brood should be extended when reproductive competition increases, as this will increase his paternity in the current brood and/or in future broods (Kvarnemo, 2006; Kahn *et al.*, 2013). In contrast, where selection disfavours males that provide care for offspring less likely to be their own, an increase in reproductive competition is expected to lead to a decrease in parental effort in the current brood.

Some empirical observations appear to support the increased paternity hypothesis [e.g. in some fish, females prefer to spawn in the nests of males already caring for eggs (Ridley & Rechten, 1981; Forsgren *et al.*, 1996)], but to our knowledge, the key prediction of the hypothesis, outlined above, has not been explicitly tested. Here we provide a test using *Nicrophorus vespilloides* burying beetles as a model system. Male and female burying beetles provide complex prenatal and postnatal parental care, either alone or together, and for uniparental care, male and female parental behaviour has been shown to increase offspring fitness (Scott, 1989; Eggert *et al.*, 1998; Smiseth *et al.*, 2003, 2007). A small vertebrate carcass is the necessary resource for rearing a single brood of offspring (Pukowski, 1933), and burying beetles often engage in direct intrasexual contests for these scarce breeding resources. Beetles that lose a contest to a dominant individual often remain and adopt a satellite (male) or brood parasitic (female) role, but the presence of these subordinate individuals introduces uncertainty over the genetic parentage of a brood for either or both parents. The extent of this uncertainty depends on the sex ratio (and number) of these subordinate competitors, which varies among reproductive events (Müller *et al.*, 1990, 2007). Eggs of a brood parasitic female (or females) reduce the dominant female's parentage but also reduce the dominant male's proportion of paternity (because the carcass can only support a finite brood) unless he mates with them and sires the resulting offspring. In contrast, satellite males represent a threat to the paternity of the dominant male by sneaking matings with the dominant

female (Scott, 1998; Müller *et al.*, 2007). These imbalances are reflected in the exclusively intrasexual fights that establish dominance at a carcass (Otronen, 1988; Lee *et al.*, 2013).

Studies on burying beetles have acknowledged the importance of intrasexual competition in determining parentage during a breeding bout (e.g. Müller & Eggert, 1989; Müller *et al.*, 2007) but have not tested the effect that variation in this competitive social environment has on parental behaviour and reproductive output together. We provide such a test here in controlled laboratory conditions designed to allow natural expression of beetle parental and social behaviour. We manipulated the sex ratio of reproductive competitors in the burying beetle *N. vespilloides* to test the critical prediction of the increased paternity hypothesis: that male care should be extended when this is likely to increase paternity (Kvarnemo, 2006). If male decisions to stay are based on returns via increased paternal care provision, males should stay longer when in a monogamous pair than when there is competition and greater duration of care should be positively correlated with parental productivity in terms of reproductive output. In contrast if, as predicted by Kvarnemo (2006), male care decisions are based on increasing paternity of current and/or future broods (e.g. securing a greater proportion of parentage via mate guarding and/or repeated mating), the opposite pattern should be seen: males will stay longer when there is intrasexual competition at the carcass with no, or negative, effects on reproductive output.

## Materials and methods

Over 200 wild beetles were caught in funnel-type bottle-traps baited with small pieces of putrescent salmon and hung in trees in a Cornish woodland, UK (SW 772 376) during the autumn of 2011. Laboratory experimental stock was generated from the outbred F4 offspring of these wild beetles. Beetles were housed individually in clear plastic boxes, maintained at a temperature of 16–20 °C with an 16-h : 8-h light : dark cycle and fed decapitated mealworms *ad libitum* from eclosion until introduced to their experimental environments, as described by Head *et al.* (2012).

Laboratory stock beetles ( $n = 246$ ) were weighed, measured and randomly assigned to one of four treatments. Each beetle within each treatment replicate was marked to enable identification of individuals. Marking was achieved by lightly scratching a small area (~1 mm Ø) on the dorsal surface of elytra with a hobby drill fine sanding bit, in one of the four distinctive orange patches of all beetles (i.e. either rear right, rear left, front right or front left), and then applying a dot of black Indian ink. The orange quarter marked was randomized for each of the four (or two) individuals within each treatment group and replicate.

The whole duration of each breeding bout was filmed in the laboratory (from the introduction of beetles to a carcass until larvae dispersed) using arenas designed for this purpose (Hopwood *et al.*, 2013). Each arena consisted of a 400 mm length of black PVC-U 110 mm Ø pipe placed upright in a 30L plasterer's bucket containing approximately 25 mm of moist compost. Three 40 mm Ø exit holes were drilled in the inner pipe 5 mm above the compost surface level (these inner pipes we refer to as 'Nicrocosms' (Hopwood *et al.*, 2013), whereas 'arena' refers to Nicrocosm and bucket combined). This design allows beetles to escape from other beetles into the outer arena and also permits caregiving beetles to desert broods at will. A closed-circuit, infrared surveillance camera (N08CX night vision CCTV camera) was positioned inside the lumen of each Nicrocosm using motion detecting software (AVerMedia NV6240 Express, DVR version 7.7.0.0007; www.avermedia-dvrs.com) to capture beetle activity around a mouse carcass that was positioned inside (see supplementary information in Hopwood *et al.*, 2013 for technical details). Experimental female beetles were mated with nonexperimental stock males 24 h before being used, as almost all (93%) sexually mature females caught in the wild have been found, in a previous study, to be predated (Müller & Eggert, 1989). This is important because it means both that wild females can breed without a male being present but also that even as part of a 'monogamous' pair wild males face a threat to paternity through stored sperm. Experimental beetles were assigned at random to treatment groups when they were between 14 and 21 days old (post-eclosion), but individuals were kept separate from one another until introduced to the arena. Mouse size was standardized (mean  $\pm$  SD = 21.16  $\pm$  0.60 g) across treatments to enable comparisons of reproductive output, and experimental beetles' pronotal width was used as a proxy for body size.

### Treatment groups

#### *Female bias (mfff)*

Three females and one male ( $n = 17$ ) had access to a single mouse carcass. The virgin male was placed in the arena with a mouse carcass, and three randomly chosen predated females, during the activity period in the afternoon (when wild beetles fly in search of carcasses).

#### *Male bias (mmmf)*

One predated female was introduced to three virgin males and a mouse carcass during the afternoon activity period ( $n = 18$ ).

#### *No sex bias (mmff)*

Two predated females and two virgin males were placed in an arena containing a mouse carcass ( $n = 17$ ).

#### *No current extrapair competition (mf)*

A virgin male and a single predated female were placed in an arena with a mouse carcass ( $n = 19$ ).

Beetle activity on and around the carcass (i.e. inside the Nicrocosm) was recorded on video from the time experimental beetles were introduced to carcasses until larval dispersal. Post-natal care duration was measured as the proportion of time that a beetle remained with the brood between the first larvae seen and larval dispersal from the carcass (individual parental desertion defined as an unbroken 6-h absence from the carcass with no parental behaviour witnessed). Number of matings was used as a measure of paternity assurance behaviour, but in contrast to previous studies (e.g. House *et al.*, 2008; Head *et al.*, 2014), matings in this experiment were recorded on video *in situ* (i.e. the beetles were not removed from the carcass) for the whole duration of reproductive bouts. Time taken to bury the carcass was used as an indication of prenatal parental performance. This was measured from the first contact with the carcass (defined as physical contact with carcass combined with exploratory behaviour, that is stopping and waving antennae or burrowing under carcass) by the caregiving female individual, to the time that only the distal half of the mouse tail remained above ground. Post-natal parental performance was measured in terms of brood size and larval mass at larval dispersal. Dominant (caregiving) beetles were designated as the male and female that repelled initial same-sex incursions on to the carcass, that subsequently engaged in prenatal preparation of the carcass, that predominantly remained inside the Nicrocosm and that became the post-natal parental care providers (except in the case of two dominant males which deserted prior to larval hatching but fulfilled the other criteria). In treatments with no same-sex competition, the uncontested caregiving beetle is designated a dominant.

### Analysis

Analyses were performed using 'r' version 2.14.1 (R Development Core Team 2011). Duration of paternal care (the proportion of total post-natal larval developmental time spent performing parental duties) was analysed using a generalized linear model with a quasi-binomial error structure (to account conservatively with overdispersion) with social treatment (four categories) as the independent variable. Male vs. female desertion (counts of whether the male or female was the first to desert among treatments) was analysed with a Fisher exact test. The effect of treatment on brood size (the number of offspring that dispersed from the carcass) was analysed using ANCOVA including larval mass as a covariate to control for the correlation between offspring number and size. Mating frequency was natural-log-transformed to normalize its distribu-

tion and analysed using linear regression with treatment as the single independent variable. The relationship between mating frequency and duration of burial (natural-log-transformed) was analysed using a linear model. Of 71 total breeding bout replicates, two failed to produce larvae and missing data-points across treatments left a sample size of 65 for post-natal care analysis and slight variation in total sample size across analyses. In all multivariate analyses, a minimal adequate model was determined through stepwise model simplification starting with a full model including all interactions and sequentially removing nonsignificant terms from the model starting with highest order interactions (Crawley, 2007). Post hoc multiple comparisons were obtained using Tukey's honest significant differences where necessary.

## Results

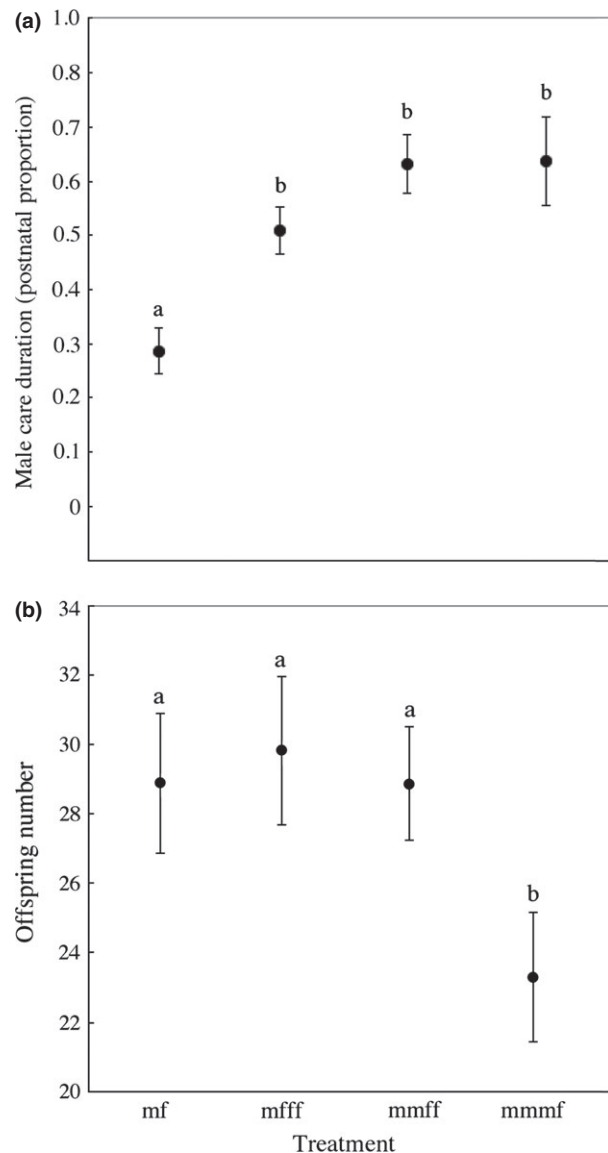
Dominant male parents adjusted their desertion decisions according to the social competitive environment experienced at a carcass: they deserted significantly earlier from monogamous pairs compared to carcasses where there was intrasexual competition (GLM with quasi-binomial error structure: treatment,  $F_{3,61} = 5.863$ ,  $P = 0.001$ , Fig. 1a). The sex of the dominant carer that deserted first was not influenced by the social competitive environment: only three males cared for longer than their female partner (i.e. < 5% of pairs) and every other dominant female remained with their brood until the larvae dispersed regardless of the nature or sex ratio of competition (Fisher exact test:  $n = 69$  pairs,  $P = 0.319$ ).

### Social environment effects on reproductive productivity

Variation in the social competitive environment affected offspring number, with fewer larvae dispersing from carcasses in the treatment with most male competitors (mmmf) (Fig. 1b). We analysed this with treatment as factor and larval size as covariate, thereby controlling for a strong trade-off between offspring number and size on a limited resource (ANCOVA, treatment,  $F_{3,62} = 3.309$ ,  $P = 0.026$ ; larval size,  $F_{1,62} = 79.4$ ,  $P < 0.0001$ ). The interaction term between treatment and larval size was not significant ( $F_{3,59} = 1.551$ ,  $P = 0.211$ ) and hence removed from the model.

### Social environment effects on mating frequency

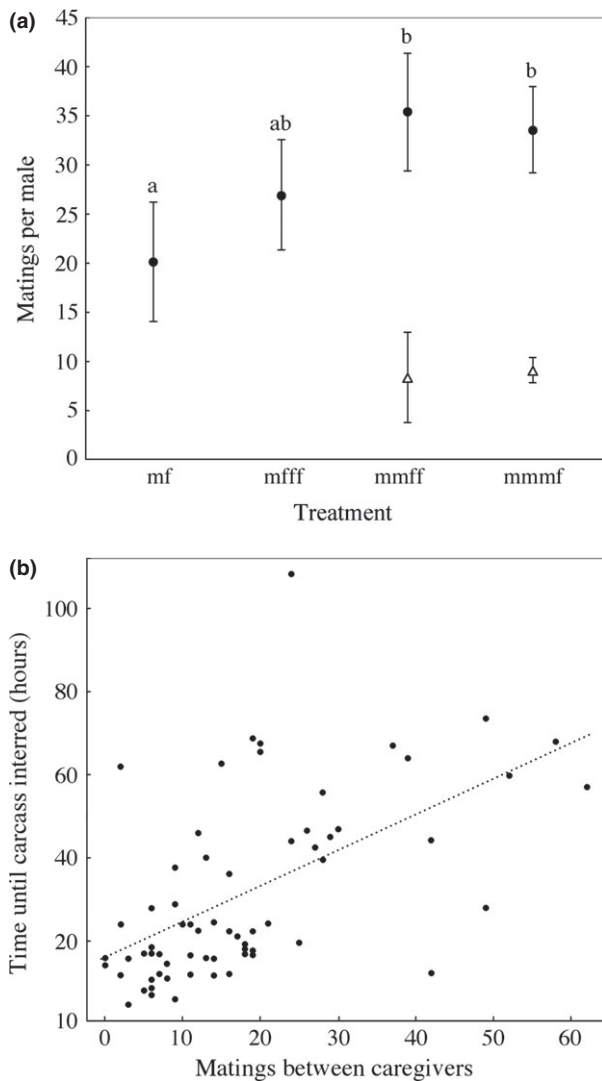
The social environment treatment affected the number of times that the focal male mated with the focal female: dominant males with male competitors present (i.e. the male bias (mmmf) and no sex bias (mmff) treatments) mated more frequently with the dominant female than did males in monogamous pairs (LM, treatment,  $F_{3,62} = 4.667$ ,  $P = 0.005$ , Fig. 2a). The corollary



**Fig. 1** (a) Mean proportion of the total post-natal larval developmental period (from first larval arrival at carcass to larval dispersal from carcass) that the dominant male remained in attendance performing parental activities. X-axis labels indicate the constituents of four different social competitive treatments (i.e. 'mf' = one male and one female; 'mfff' = one male and three females; 'mmff' = two males and two females; 'mmmf' = three males and one female); (b) effect of treatment on brood size at larval dispersal. Lower case letters above error bars indicate significant differences among treatment groups.

of this was that dominant females in treatments with male-male competition experienced approximately twice the overall mating frequency (i.e. including matings with subordinate males) than did those in pairs without additional competitors (mf =  $20.12 \pm 6.08$ ; mfff =  $26.94 \pm 5.62$ ; mmff =  $43.69 \pm 9.70$ ; mmmf =  $42.65 \pm 4.72$  times per hour, mean  $\pm$  SD; LM,





**Fig. 2** (a) Dominant male matings with dominant female (filled circles), and subordinate male matings with dominant female (open triangles), lower case letters indicate significant differences between treatments; (b) positive relationship between hours taken to bury carcass (y-axis) and frequency of mating between pairs of caregiving beetles (x-axis). Figure shows least squares regression on untransformed data for illustration purposes.

treatment,  $F_{3,65} = 6.114$ ,  $P < 0.001$ , see also Fig. 2a). In the two treatments with male competitors, mating frequency of the dominant male was significantly greater than that of subordinates (Wilcoxon signed rank test, dominant status,  $V = 525$ ,  $n = 37$ ,  $P < 0.0001$ , Fig. 2a).

### Effects of mating frequency on carcass burial speed

Increased preburial mating frequency prolonged carcass burial (linear regression:  $\log(\text{carcass burial})$ ,  $F_{1,65} = 31.302$ ,  $P < 0.0001$ ,  $R^2 = 0.31$ , Fig. 2b).

## Discussion

We found males that faced competition not just from males, but also from females, extended the duration of time they remained with their partners and the brood compared to males in monogamous pairs (Fig. 1a). Males in treatments with satellite male competition mated more frequently with the dominant female than did those in treatments with no satellite males present (Fig. 2a). By staying longer and increasing his mating frequency, a caregiving male maximizes his current paternity against the success of subordinate satellite males (Müller & Eggert, 1989; House *et al.*, 2008). He also has the opportunity, by mating with subdominant (brood parasitic) females, to improve his current paternity proportion and potentially secure paternity in their future broods. Kvarnemo's (2006) model explicitly suggests that male care may evolve when there is a net benefit resulting from the combined sum of three factors: (a) gained or lost opportunities for mating, (b) increased paternity and (c) improved offspring fitness. We found that potential benefits for males via resource guarding and paternity protection may come at a cost for females through higher mating frequency (see Head *et al.*, 2014). We discuss the likely role of these factors in the evolution of male care below.

### Opportunities for mating

In many species, opportunities for mating are reduced for caregiving males, but this is not always the case [e.g. in nest-building fish species where males caring for eggs are preferred by spawning females (Ridley & Rechten, 1981; Forsgren *et al.*, 1996; Alonzo, 2008)]. In burying beetles, reproductive success has been viewed as resource limited rather than mate limited (Scott, 1998). This is because although males can call (release pheromones) for females and mate without finding a carcass, matings are only translated into reproductive success when a female subsequently finds a carcass (Müller *et al.*, 2007). However, when competition occurs at a carcass, reproductive success can be mate limited to an extent because subordinates do not have the same opportunities to mate. When a premated female locates a carcass, she may breed alone, but a male finding a carcass must first call a female (Eggert & Müller, 1989). This is important because it means the dominant male at a carcass has a potential route to future reproductive success even while engaged in caregiving. He can replenish the sperm stored by his female partner and any subordinate females that visit. Therefore, by prolonging paternal care, the apparent cost of his lost mating opportunities can be ameliorated by the likelihood that another carcass is located by the current (proven) female breeding partner(s).

### Increased paternity

Kvarnemo (2006) points out that the benefits from increased paternity may be divided into current and future benefits. Males of some nest-building goby species line the inside of their nest (where females lay eggs) with sperm-infused mucus helping to improve the current paternity of the caring male against rival sneaker males' sperm (Scaggiante *et al.*, 2005; Svensson & Kvarnemo, 2005, 2007). A study of savannah sparrows, *Passerculus sandwichensis*, provides an example of a future paternity benefit of current paternal caregiving: male parents that were attentive to a first brood were rewarded by their mates with higher paternity (through higher female fidelity) in their second broods (Freeman-Gallant, 1996). Male burying beetles can maximize their current paternity (to above 90%) when it is challenged by male rivals who are present (satellites) or absent (stored sperm in predated females) by repeatedly mating with females (Müller & Eggert, 1989). Sperm precedence in *N. vespilloides* is an increasing function of repeated mating, but a male may have to mate seven times even to gain 50% paternity when a female has been predated (Müller & Eggert, 1989; House *et al.*, 2008). Thus, dominant *N. vespilloides* males sharing a carcass with a female in the wild can reduce the proportion of larvae sired by other males that employ alternative male tactics (i.e. males having called and mated with females without first finding a carcass or satellite males; Müller *et al.*, 2007). When a male encounters more than one female at a carcass (e.g. our 'mfff' and 'mmff' treatments), subordinate females lay eggs near the carcass and unless mated by him, they will use stored sperm from rival and/or absent male(s). In this situation, the caregiving male, by staying and mating with all females present, has an opportunity to improve his current and future reproductive success. This is because any females with whom he has mated – especially those that find a carcass and breed alone in the future – have the potential to produce future broods using his sperm.

Female stored sperm has a limited lifespan, starting to become unviable after three weeks (Eggert, 1992), so males that delay their desertion from the current breeding bout may increase their future success by ensuring the departing dominant female has freshly replenished sperm stores. In this study, males continued to mate beyond the time when eggs were laid, and even larvae hatched, and those facing threats to their paternity extended their care period. Males across all treatments were observed mating after larvae hatched (mf =  $1 \pm 0.41$ ; mfff =  $3.88 \pm 1.83$ ; mmff =  $4.75 \pm 1.82$ ; mmmf =  $3.47 \pm 1.23$  matings, mean  $\pm$  SD). These matings could have little or no benefit to either sex with respect to the current brood, but this prolonged residence with repeated mating could influence a male's future paternity when females inseminated by

him (during the current breeding bout) find new breeding opportunities. This may be an important component of his future reproductive success because the incidence of females breeding without males can be high in nature. A study in which 300 mouse carcasses were placed in the wild found 39% (100 of 258) that were buried by beetles had only *N. vespilloides* females present (Eggert, 1992).

In our study, dominant males mated with sufficient frequency (i.e. more than seven times) to achieve a high proportion of paternity in treatments with a single (potentially predated) dominant female. The frequency with which the dominant male and female mated increased in the presence of satellite males, as would be predicted if males are defending their paternity (Fig. 2a). The mean prenatal mating frequency we recorded between dominant individuals, from their first contact with each other to burial of the carcass, was  $15.1 \pm 12.7$  matings per hour (mean  $\pm$  SD) [over a mean period of  $25 \pm 18$  h (mean  $\pm$  SD)]. The dominant male invariably copulated with the dominant female immediately after a satellite male was encountered, regardless of whether or not a successful satellite mating had occurred (P.E. Hopwood, personal observation). As a result dominant females were mated almost twice as frequently (in total) in groups with multiple males compared to groups with a single male. A recent study showed that female *N. vespilloides* suffer costs of repeated mating that affect the provision of maternal care, leading to reduced offspring performance (Head *et al.*, 2014). Thus, optimal mating rate for females – for whom there appears to be no fitness advantage beyond two matings (House *et al.*, 2008, 2009) – conflicts with that of males who may secure an important component of future paternity by mating frequently during the current reproductive bout, especially if his female partner subsequently breeds alone, using stored sperm (Eggert, 1992). Another cost associated with increased mating frequency is the overall time taken for carcass burial (Fig. 2b). It is not clear whether this occurred because males were distracted from helping with carcass burial or because dominant females suffered interference from resistance to the intrusions of dominant males eager to up-regulate their mating frequency. Nevertheless, a potential cost of increased mating rate, driven by males in response to threats to paternity from other males, is to increase the risk of usurpation by a larger same-sex conspecific competitor or total loss of the breeding resource to other competitors or scavengers through increasing the time to successfully bury the carcass (Scott, 1990; Müller *et al.*, 1998; Trumbo, 2007).

Brood size was smallest in the treatment with the most male competition despite these dominant males' prolonged post-natal brood attendance compared to males without threats to their paternity assurance. Cues indicating a low proportion of brood parentage for a caregiving female (i.e. the female-biased treatment)

might have been predicted to induce early female desertion, leaving the male to care uniparentally. For example, in penduline tits, *Remiz pendulinus*, either the male or the female is impelled to provide uniparental care for a brood by the early desertion of their partner (van Dijk *et al.*, 2012). However, we found no evidence that variation in parentage assurance between sexes determined which sex deserted first; in only three cases (out of 69) males deserted before females.

One alternative explanation for the pattern of male residence with the brood is resource competition in the face of high competitor density. In our design, the caregiving female has already established and maintained dominance status against female competitors present (usually by virtue of a size advantage). We think that if resource guarding against risk of brood takeover was the primary factor explaining variation in male duration of care, males in both treatments without male competitors (i.e. mf and mfff) should be expected to desert early because as long as the lone male has mated sufficiently with any subordinate females present, the current brood will be comprised of his offspring whether or not the dominant female is subsequently usurped by these female rivals. In field studies of a wild population of *N. vespilloides*, we have recorded a very low incidence of intruding beetles arriving after carcass burial. In approximately 220 witnessed *N. vespilloides* reproductive events to-date, only three were recorded with an intruding beetle arriving after carcass burial was complete (P.E. Hopwood, unpublished). Nonetheless, studies of other species support the idea that increased likelihood of current brood success via resource guarding may select for extended male attendance in biparental care at least where intruders sometimes arrive in later stages of reproductive bouts [e.g. *Nicrophorus orbicollis*: (Scott, 1990; Trumbo, 1991); *Nicrophorus defodiens*: (Eggert & Sakaluk, 2000); *Nicrophorus pustulatus*: (Trumbo, 2007)].

### Offspring benefits

Benefits to fathers through increased paternity need not be exclusive of offspring benefits. One puzzle is that although biparental care is the most common parental association in burying beetles (and both partners share all post-natal parental duties), no clear benefit to offspring has been found for biparental care over uniparental care from either sex (Müller *et al.*, 1998; Smiseth *et al.*, 2005). An additional benefit to offspring via a male's contribution to parental care is not a prerequisite of Kvarnemo's (2006) hypothesis, which proposes that male care can evolve as long as there is a net benefit to males via increased paternity and/or mating opportunities. We found no relationship between male duration of care and brood size, but rather, there appeared to be an inverse relationship between variation in brood size and the level of intrasexual competition males

experienced (Fig. 1b). Artificial selection for increased repeated mating rate has also been shown to affect the quality of female parental care provision leading to reduced offspring performance (Head *et al.*, 2014). Here we show that the mating frequency experienced by caregiving females has a social environmental component: mating increased in response to threats to male paternity assurance.

### Conclusions

Male *N. vespilloides* parents responded to experimentally manipulated variation in the local competitive social environment: When cues indicated reduced paternity assurance, caregiving males increased the duration of time they stayed with their partner during the period of parental care and they responded to threats to paternity by increasing mating frequency. Threats to paternity come from direct competition from additional males and from sperm competition with absent males with whom the female had previously mated, but also from brood parasitic females who have the potential to lay eggs fertilized with the stored sperm of absent males. Males in monogamous partnerships (i.e. with no extrapair competition) exhibited the shortest duration of care, despite having the greatest confidence in paternity. Collectively, results support the hypothesis that males may prolong the time they spend with their partner and the brood when by doing so they can benefit from increased paternity (Kvarnemo, 2006). However, variation in the competitive social environment experienced by individuals appears to affect the intensity of sexual conflict between parents. The evolution of patterns of parental investment between sexes in this and other species with biparental or male uniparental care reflects a balance between sexual selection (e.g. direct benefit to males via increasing mating success vs. costs to females of increased mating) and natural selection (e.g. direct benefits of male parental care contribution vs. indirect costs in terms of reduced offspring fitness and brood safety).

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### References

- Alonzo, S.H. 2008. Female mate choice copying affects sexual selection in wild populations of the ocellated wrasse. *Anim. Behav.* **75**: 1715–1723.

- Alonzo, S.H. 2010. Social and coevolutionary feedbacks between mating and parental investment. *Trends Ecol. Evol.* **25**: 99–108.
- Alonzo, S.H. & Klug, H. 2012. Paternity, maternity, and parental care. In: *The Evolution of Parental Care* (N.J. Royle, P.T. Smiseth & M. Kölliker, eds), pp. 189–205. Oxford University Press, Oxford.
- Benowitz, K.M., Head, M.L., Williams, C.A., Moore, A.J. & Royle, N.J. 2013. Male age mediates reproductive investment and response to paternity assurance. *Proc. R. Soc. B* **280**: 20131667.
- Birkhead, T.R. 1979. Mate guarding in the magpie *Pica pica*. *Anim. Behav.* **27**: 866–874.
- Birkhead, T.R. 1982. Timing and duration of mate guarding in magpies, *Pica pica*. *Anim. Behav.* **30**: 277–283.
- Burke, T., Davies, N.B., Bruford, M.W. & Hatchwell, B.J. 1989. Parental care and mating behaviour of polyandrous dunlocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* **338**: 249–251.
- Clutton-Brock, T.H. & Vincent, A.C.J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature* **351**: 58–60.
- Crawley, M.J. 2007. *The R Book*. Wiley and Sons, Chichester.
- van Dijk, R.E., Székely, T., Komdeur, J., Pogány, Á., Fawcett, T.W. & Weissing, F.J. 2012. Individual variation and the resolution of conflict over parental care in penduline tits. *Proc. R. Soc. B* **279**: 1927–1936.
- Eggert, A.K. 1992. Alternative male mate-finding tactics in burying beetles. *Behav. Ecol.* **3**: 243–254.
- Eggert, A.K. & Müller, J.K. 1989. Mating success of pheromone-emitting *Necrophorus* males: do attracted females discriminate against resource owners? *Behaviour* **110**: 248–257.
- Eggert, A.K. & Sakaluk, S.K. 2000. Benefits of communal breeding in burying beetles: a field experiment. *Ecol. Entomol.* **25**: 262–266.
- Eggert, A.K., Reinking, M. & Müller, J.K. 1998. Parental care improves offspring survival and growth in burying beetles. *Anim. Behav.* **55**: 97–107.
- Forsgren, E., Karlsson, A. & Kvarnemo, C. 1996. Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behav. Ecol. Sociobiol.* **39**: 91–96.
- Freeman-Gallant, C.R. 1996. DNA fingerprinting reveals female preference for male parental care in savannah sparrows. *Proc. R. Soc. B* **263**: 157–160.
- Griffin, A.S., Alonzo, S.H. & Cornwallis, C.K. 2013. Why do cuckolded males provide paternal care? *PLoS Biol.* **11**: e1001520.
- Harrison, F., Barta, Z., Cuthill, I. & Székely, T. 2009. How is sexual conflict over parental care resolved? A meta-analysis. *J. Evol. Biol.* **22**: 1800–1812.
- Hartley, I.R., Davies, N.B., Hatchwell, B.J., Desrochers, A., Nebel, D. & Burke, T. 1995. The polygynandrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and parental effort. *Anim. Behav.* **49**: 789–803.
- Head, M.L., Berry, L.K., Royle, N.J. & Moore, A.J. 2012. Paternal Care: direct and indirect genetic effects of fathers on offspring performance. *Evolution* **66**: 3570–3581.
- Head, M.L., Hinde, C.A., Moore, A.J. & Royle, N.J. 2014. Correlated evolution in parental care in females but not males in response to selection on paternity assurance behaviour. *Ecol. Lett.* **17**: 803–810.
- Hopwood, P.E., Moore, A.J. & Royle, N.J. 2013. Nutrition during sexual maturation affects competitive ability but not reproductive productivity in burying beetles. *Funct. Ecol.* **27**: 1350–1357.
- House, C.M., Evans, G., Smiseth, P.T., Stamper, C.E., Walling, C.A. & Moore, A.J. 2008. The evolution of repeated mating in the burying beetle, *Nicrophorus vespilloides*. *Evolution* **62**: 2004–2014.
- House, C.M., Walling, C.A., Stamper, C.E. & Moore, A.J. 2009. Females benefit from multiple mating but not multiple mates in the burying beetle *Nicrophorus vespilloides*. *J. Evol. Biol.* **22**: 1961–1966.
- Houston, A.I. 1995. Parental effort and paternity. *Anim. Behav.* **50**: 1635–1644.
- Hunt, J. & Simmons, L.W. 2002. Confidence of paternity and paternal care: covariation revealed through the experimental manipulation of the mating system in the beetle *Onthophagus taurus*. *J. Evol. Biol.* **15**: 784–795.
- Kahn, A.T., Schwanz, L.E. & Kokko, H. 2013. Paternity protection can provide a kick-start for the evolution of male-only parental care. *Evolution* **67**: 2207–2217.
- Kokko, H. & Jennions, M. 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**: 919–948.
- Kokko, H. & Jennions, M. 2012. Sex differences in parental care. In: *The Evolution of Parental Care* (N. Royle, P. Smiseth & M. Kölliker, eds), pp. 101–116. Oxford University Press, Oxford.
- Kvarnemo, C. 2006. Evolution and maintenance of male care: is increased paternity a neglected benefit of care? *Behav. Ecol.* **17**: 144–148.
- Lee, V.E., Head, M.L., Carter, M.J. & Royle, N.J. 2013. Effects of age and experience on contest behaviour in the burying beetle, *Nicrophorus vespilloides*. *Behav. Ecol.* **25**: 172–179.
- Müller, J.K. & Eggert, A.K. 1989. Paternity assurance by “helpful” males: adaptations to sperm competition in burying beetles. *Behav. Ecol. Sociobiol.* **24**: 245–249.
- Müller, J.K., Eggert, A.K. & Dressel, J. 1990. Intraspecific brood parasitism in the burying beetle, *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Anim. Behav.* **40**: 491–499.
- Müller, J.K., Eggert, A.K. & Sakaluk, S.K. 1998. Carcass maintenance and biparental brood care in burying beetles: are males redundant? *Ecol. Entomol.* **23**: 195–200.
- Müller, J.K., Braunisch, V., Hwang, W. & Eggert, A.K. 2007. Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*. *Behav. Ecol.* **18**: 196–203.
- Otronen, M. 1988. The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Ann. Zool. Fenn.* **25**: 191–201.
- Parker, G.A., Royle, N.J. & Hartley, I.R. 2002. Intrafamilial conflict and parental investment: a synthesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **357**: 295–307.
- Pukowski, E. 1933. Ökologische untersuchungen an *Necrophorus* F. *Zoomorphology* **27**: 518–586.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Ridley, M. & Rechten, C. 1981. Female sticklebacks prefer to spawn with males whose nests contain eggs. *Behaviour* **76**: 152–161.



- Royle, N.J., Hartley, I.R. & Parker, G.A. 2002. Sexual conflict reduces offspring fitness in zebra finches. *Nature* **416**: 733–736.
- Royle, N.J., Smiseth, P.T. & Kölliker, M. 2012. *The Evolution of Parental Care*. Oxford University Press, Oxford.
- Scaggiante, M., Rasotto, M.B., Romualdi, C. & Pilastro, A. 2005. Territorial male gobies respond aggressively to sneakers but do not adjust their sperm expenditure. *Behav. Ecol.* **16**: 1001–1007.
- Scott, M.P. 1989. Male parental care and reproductive success in the burying beetle, *Nicrophorus orbicollis*. *J. Insect Behav.* **2**: 133–137.
- Scott, M.P. 1990. Brood guarding and the evolution of male parental care in burying beetles. *Behav. Ecol. Sociobiol.* **26**: 31–39.
- Scott, M.P. 1998. The ecology and behavior of burying beetles. *Annu. Rev. Entomol.* **43**: 595–618.
- Sheldon, B.C. 2002. Relating paternity to paternal care. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **357**: 341–350.
- Smiseth, P.T., Darwell, C.T. & Moore, A.J. 2003. Partial begging: an empirical model for the early evolution of offspring signalling. *Proc. R. Soc. B* **270**: 1773–1777.
- Smiseth, P.T., Dawson, C., Varley, E. & Moore, A.J. 2005. How do caring parents respond to mate loss? Differential response by males and females. *Anim. Behav.* **69**: 551–559.
- Smiseth, P.T., Lennox, L. & Moore, A.J. 2007. Interaction between parental care and sibling competition: parents enhance offspring growth and exacerbate sibling competition. *Evolution* **61**: 2331–2339.
- Svensson, O. & Kvarnemo, C. 2005. The importance of sperm competition risk and nest appearance for male behavior and female choice in the sand goby, *Pomatoschistus minutus*. *Behav. Ecol.* **16**: 1042–1048.
- Svensson, O. & Kvarnemo, C. 2007. Parasitic spawning in sand gobies: an experimental assessment of nest-opening size, sneaker male cues, paternity, and filial cannibalism. *Behav. Ecol.* **18**: 410–419.
- Trivers, R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (B.G. Campbell, ed.), pp. 136–179. Aldine, Chicago.
- Trumbo, S.T. 1991. Reproductive benefits and the duration of paternal care in a biparental burying beetle, *Nicrophorus orbicollis*. *Behaviour* **117**: 82–105.
- Trumbo, S.T. 2007. Defending young biparentally: female risk-taking with and without a male in the burying beetle, *Nicrophorus pustulatus*. *Behav. Ecol. Sociobiol.* **61**: 1717–1723.
- Whittingham, L.A., Taylor, P.D. & Robertson, R.J. 1992. Confidence of paternity and male parental care. *Am. Nat.* **139**: 1115–1125.

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